

A PRIMITIVE CRICETID (MAMMALIA: RODENTIA) FROM THE MIDDLE EOCENE OF JIANGSU PROVINCE, CHINA

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ABSTRACT

A new species of the cricetid rodent *Pappocricetodon*, *P. antiquus*, from Middle Eocene fissure deposits in southeastern China combines such derived features as uniserial incisor enamel and a hystricomorphous zygomatic structure with primitive characters including retention of P⁴ and less expansion of the anterocone/id of M¹/M₁ than in other species of the genus. This addition to the Eocene record of myomorph rodents lends support to the hypothesis that the most likely sister group of the Myomorpha is the family Sciuravidae.

INTRODUCTION

The Cricetidae, one of the most flourishing families of living rodents in the world, are known to have diversified and dispersed in the Holarctic since latest Eocene times. Due to their abundance in the fossil record, cricetids have been used in the subdivision and correlation of Cenozoic Holarctic continental deposits (Fahlbusch, 1964; Mein, 1975; Engesser, 1985). This abundance has also led to numerous investigations of evolution within the family (Mein and Freudenthal, 1971a; Lindsay, 1968, 1977; Martin, 1980). Although the origin and interrelationships of the cricetids have been discussed frequently, the source of the family has been unclear. Suggested relationships have been with the Sciuravidae (Schaub, 1925; Wilson, 1949b; Wood, 1959; Martin, 1980; Walton, 1993) or with the ctenodactyloids (Lindsay, 1977; Flynn et al., 1985; Vianey-Liaud, 1985; Wang and Meng, 1986).

Part of the difficulty of studying the origin of the family has been the lack of good middle and early late Eocene records for the family. For many years this record consisted of two lower molars referred to *Cricetodon schaubi* from the Late Eocene River Section of Shanxi Province, China (Zdansky, 1930). Recently, the new genus *Pappocricetodon* was described from China, with two species: *P. rencunensis* from the late middle Eocene (Rencun Member, Hedi Formation) of Henan; and *P. schaubi*, for Zdansky's species, from the late Eocene (Zhaili Member, Hedi Formation) of Shanxi (Tong, 1992).

From 1987 to 1992 a field party from the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Academia Sinica (Qi et al., 1991), and, from 1993, a cooperative field team from the IVPP and the Carnegie Museum of Natural History (CM) collected a variety of fossil mammals from fissure fillings in the Triassic Shangqinglong Limestone in the Shanghuang Quarry of Liyang County, Jiangsu Province, China (Fig. 1). To date five fissures (IVPP Locs. 93006.A-E)

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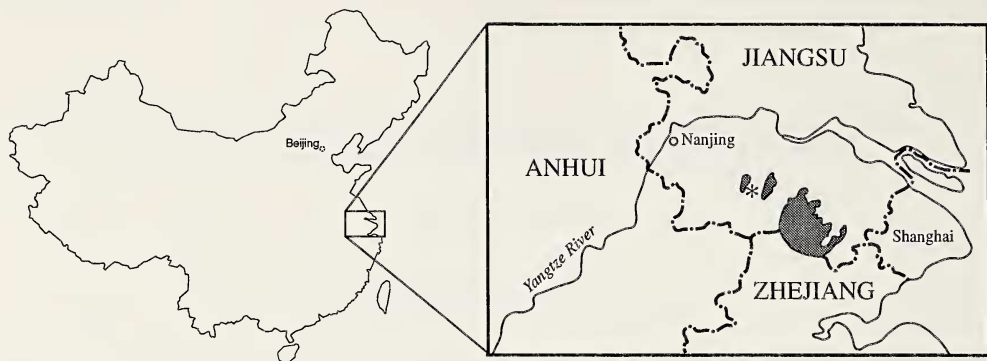


Fig. 1.—Map of China with enlargement showing parts of Jiangsu and adjoining provinces and location (*) of Shanghuang Quarry, Liyang County.

have been found to contain Paleogene deposits. In Fissure D (IVPP Loc. 93006.D) the deposits, composed mostly of red clay with lesser amounts of yellow clay, are rich in fossil mammals. Cricetid fossils dominate in Fissure D. In addition to the cricetids, the fossil mammals include varied insectivores, omomyids, leporids, *Yuomys* sp., ctenodactyloids, creodonts, *Archaeomeryx* sp., Anthracotheriidae, Homacodontidae, *Eoentelodon*, cf. *Helohyus*, brontotheres, palaeotheres, and tapiroids. All the specimens were collected by quarrying followed by screen washing. The total mammal fauna from Fissure D suggests a middle Eocene age. The Cricetidae is represented by the most primitive known and probably oldest member of the family, described here as a new species of *Pappocricetodon*.

The discovery of this primitive cricetid from the middle Eocene both reveals some primitive features and provides some suggestions on the origin of the Cricetidae and on evolutionary trends within the family.

METHODS

Figure 2 illustrates basic terminology used here for cricetid molars, combining conventional rodent dental terminology (e.g., Wood and Wilson, 1936; Mein and Freudenthal, 1971*b*) with nomenclature necessitated by the primitive features of these rodents and the opportunity to employ terms suggesting dental homology. For example, on M^1 the crest that extends anterobuccally from the protocone is termed protoloph, instead of "anterior arm of protocone" (Fahlbusch, 1964; Vianey-Liaud, 1979) because it appears homologous to the protoloph of more primitive rodents such as sciuravids. The cusp on the lingual part of the anterior cingulum, the anterocone of Lillegraven and Wilson (1975), is named the anterostyle, and their parastyle is named the anterocone. "Mure" is used for the anterior arm of the hypocone whether or not it joins the protocone. The "sinus" of the upper molar (Mein and Freudenthal, 1971*b*; Vianey-Liaud, 1979) is called "lingual valley." On the lower molars the anterior arm of the protoconid is termed the protolophid and the buccal crest of the metaconid, the metalophid.

Biostratigraphic terminology for Oligocene localities follows Wang (1992) as the most recent treatment of this interval in Asia.

Measurements were all taken by Wang using a micrometer in a Wild binocular microscope. For consistency only the left side was measured for well-represented teeth; the scarcer $M3/3$ were all measured.

In the tooth descriptions, frequency of a character variant is expressed as a ratio, with the upper number indicating presence of the variant and the lower number, total number of specimens showing the character. Thus, 101/143 indicates that out of 143 specimens, 101 have the variant described.

Abbreviations for repositories are: AMNH, American Museum of Natural History; CM, Carnegie Museum of Natural History; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology. Tables of measurements (in millimeters, mm) of the dentition utilize the positional abbreviations: L, length;

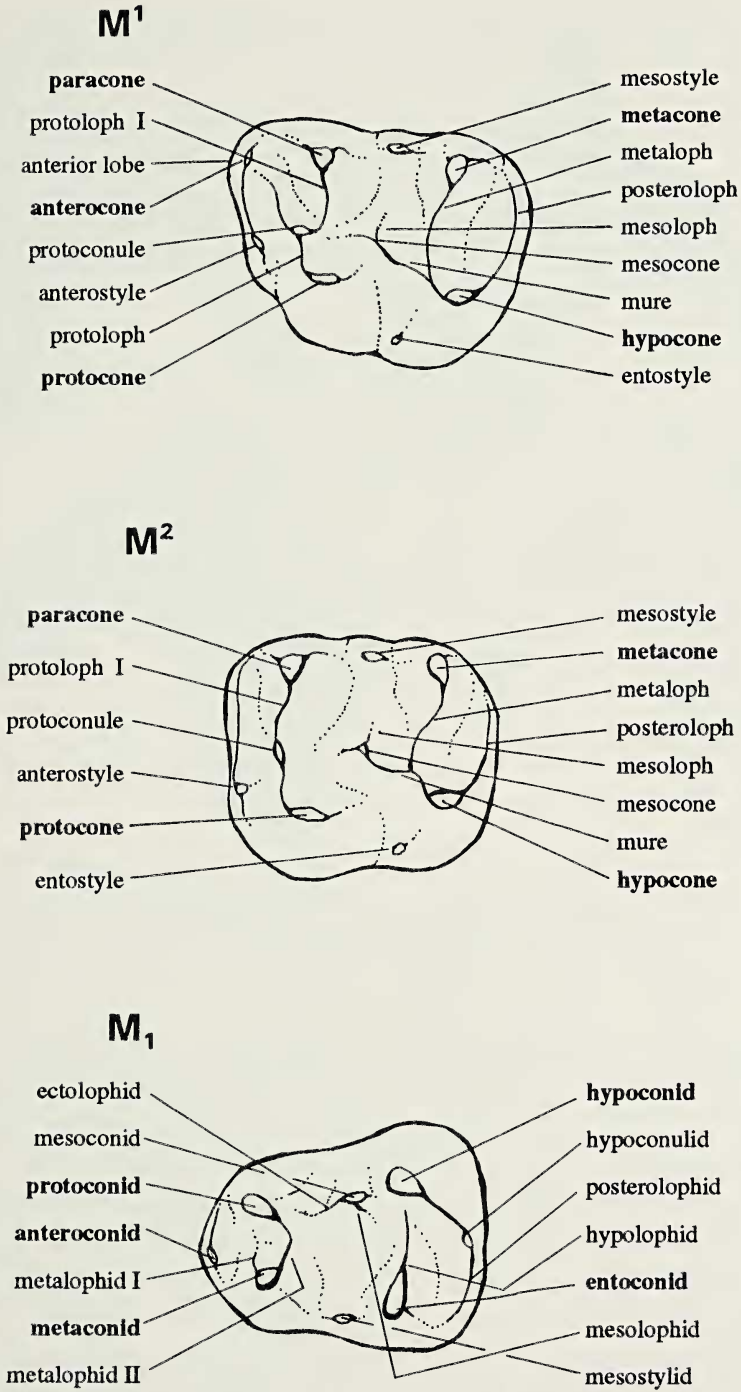


Fig. 2.—Terminology used for cricetid molars, showing simplified left M¹ and M², and right M₁.

W, width; b, buccal; l, lingual. For statistical treatment, abbreviations used are: *n*, number of specimens; O.R., observed range; \bar{x} , mean; *s*, standard deviation; C.V., coefficient of variation.

SYSTEMATICS

Order Rodentia Bowdich, 1821
 Superfamily Muroidea Miller and Gidley, 1918
 Family Cricetidae Rochebrune, 1883
Pappocricetodon Tong, 1992
Pappocricetodon antiquus, new species
 (Table 1)

Holotype.—LM¹ (IVPP V 11018.1).

Referred Specimens.—142 M¹ (IVPP V 11018.2–V 11018.143), 144 M² (IVPP V 11018.144–V 11018.287), 21 M³ (IVPP V 11018.288–V 11018.308), one left lower jaw with I₁ and M₁ (IVPP V 11018.309), one left lower jaw with M₁ (IVPP V 11018.310), one right lower jaw with M₁₋₂ (IVPP V 11018.311), 111 M₁ (IVPP V 11018.312–V 11018.422), 151 M₂ (IVPP V 11018.423–V 11018.573), 30 M₃ (IVPP V 11018.574–V 11018.603), 4 maxillae (IVPP V 11018.604–V 11018.607), 3 lower jaws (IVPP V 11018.608–V 11018.610) and 2 I₁ (IVPP V 11018.611–V 11018.612).

Diagnosis.—Cricetid smaller than *P. rencunensis*, with hystricomorphous skull and sciurognathous lower jaw; dental formula: 1/1, 0/0, 1/0, 3/3; cheek teeth brachydont; upper molars have protocone bulbous and mesoloph short; M¹ less enlarged, having anterior lobe weak and anterocone small, protoloph I weak and usually connecting to protoloph, protoloph II absent; on M¹⁻² mure usually long, lingual valley long and oblique; M³ less reduced than in other species of genus, with distinct metacone and somewhat reduced but less buccad hypocone; lower molars usually lacking ectomesolophid; M₁ less enlarged with anteroconid small and usually isolated; on M₁₋₂ hypolophid transverse, connecting to hypoconid or its posterior arm; lower incisor with uniserial enamel.

Etymology.—From Latin, *antiquus*, ancient, old.

Description.—Four edentulous maxillae of *Pappocricetodon antiquus* show that the infraorbital foramen is relatively large and rounded with no ventral constriction. This is the hystricomorphous condition. There is no bony septum isolating a neurovascular canal such as occurs in dipodoids. The ventral root of the zygomatic process extends laterally well anterior to P⁴ and is compressed dorso-ventrally. The zygomatic plate is flattened and nearly horizontal. It is bordered anteriorly and laterally by a crescentic ridge extending from anterior to P⁴ to the lateral edge of the zygoma. This configuration resembles that of *Cricetops*, an Asian cricetid, and a dipodoid such as *Zapus* more closely than that of a North American murid such as *Eumys*. This suggests that in *Pappocricetodon* the superficial and lateral branches of the masseter muscle were incompletely differentiated as in dipodoids (Klingener, 1964). The posterior part of the incisive foramen, preserved in three of the four specimens, terminates anterior to P⁴ and posterior to the anterior side of the ventral zygomatic root. The premaxillary-maxillary suture extends obliquely back and down to intersect the lateral side of the incisive foramen. The foramen appears to be relatively wider posteriorly than in *Eumys*. The anterior edge of the maxillary-palatine suture is approximately in line with the juncture of M¹ and M².

One of the interesting features of the four maxillary fragments is evidence on the dental formula of *Pappocricetodon*, unknown in the previously described species of the genus (Fig. 3). M¹ and M² each have three alveoli, one for a large lingual root and two for smaller buccal roots. These alveoli show that the anterobuccal root of M¹ protrudes anteriorly more than does the corresponding root of M². On all maxillae there is a small circular alveolus just anterior to the anterobuccal alveolus of M¹, indicating that a small tooth, P⁴ or dP⁴, occurred in front of M¹.

The anterior alveolar foramen (terminology follows Wahlert, 1974) pierces the maxilla in line with the posterior margin of the ventral zygomatic root. Behind it are nutrient foramina. The larger sphenopalatine foramen is at the anterior edge of the maxillary-palatine suture and above the intersection of M¹ and M².

Six incomplete lower jaws are known, of which three have teeth (V 11018.309; V 11018.310; V 11018.311). The horizontal ramus of the mandible is sturdy and the diastema is short (Fig. 4). The

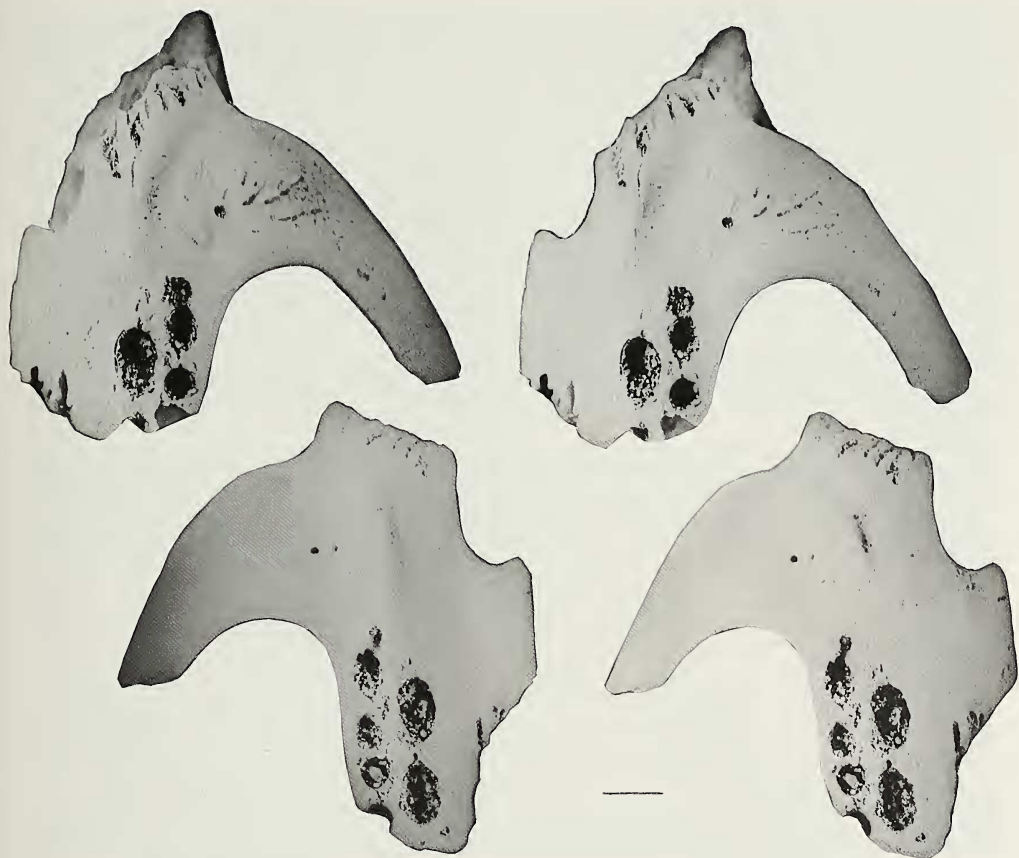


Fig. 3.—Ventral view of edentulous maxillae of *Pappocricetodon antiquus*, stereo views. Above, left maxilla, IVPP V 11018.606, showing alveoli of P⁴ (or dP⁴) and M¹. Below, right maxilla, IVPP V 11018.604, showing alveoli of P⁴ (or dP⁴), M¹, and M². Scale bar equals 1 mm.

mental foramen is anterior to M₁ and slightly above middepth of the jaw. The masseteric fossa extends forward to below M₂. Distinct upper and lower ridges form boundaries of the fossa, intersect anteriorly, and extend as a distinct ridge to below M₁. The jaw is sciurognathous.

A complete cheek tooth series is not yet known. In addition to indications from the alveoli for presence of P⁴ (or dP⁴), further evidence for the presence of a tooth anterior to M¹ comes from V 11018.90, M¹ which has a small wear facet on its anterior side. Thus, the dental formula of *Pappocricetodon antiquus* was $\frac{1.0.1.3}{1.0.0.3}$, occurring only in this genus among the Cricetidae.

The lower incisor, compressed transversely and long oval-shaped in cross section, extends into the ascending ramus. Enamel extends up to about one third of the lateral side but barely curves onto the medial side. The enamel surface has fine longitudinal ridges as in *P. rencunensis* and *P. schaubi*. Scanning electron microscope examination of the enamel of the lower incisor by Prof. Wighart von Koenigswald (letter, 17 December 1993) produced the following results (Fig. 5): "The enamel is fairly thin and has some external ridges. As normal in rodents the Portio interna (PI) and the Portio externa (PE) are well distinguishable. The PE holds only 1% of the enamel thickness. It is formed by radial enamel and the outer ridges are exclusively formed by a thickening of the PE. The interprismatic matrix is at an angle toward the prisms and anastomoses between them. The PI is built of transversely oriented uniserial Hunter-Schreger-Bands (HSB), which are vertical to the enamel dentine junction (EDJ) in a longitudinal section. In the transverse section the prisms decussate at almost right angles. The interprismatic matrix (IPM) is parallel to the prisms."

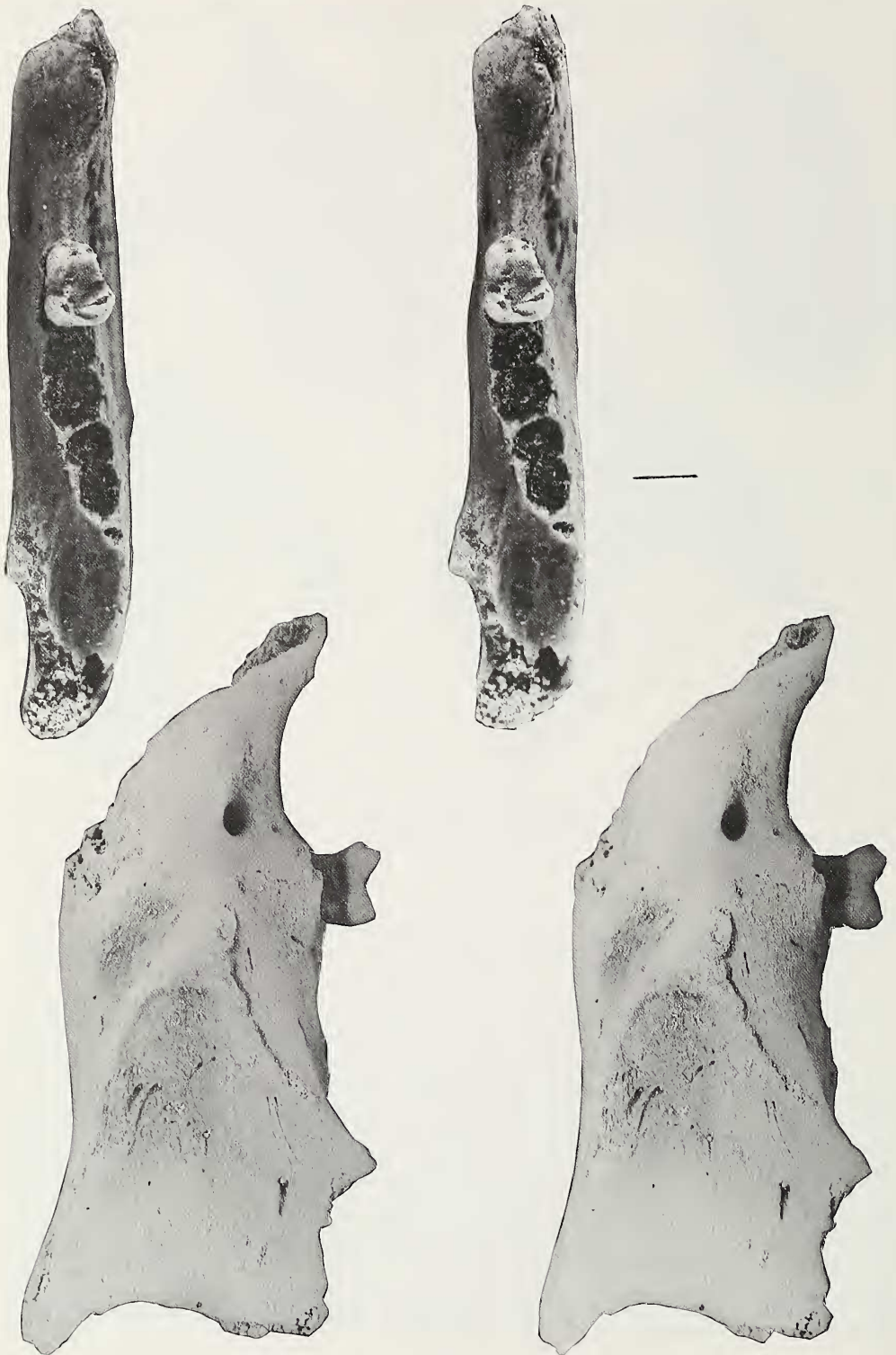


Fig. 4.—Left mandible of *Pappocricetodon antiquus*, with M_1 , IVPP V 11018.310, stereo views. Above, occlusal view showing M_1 ; below, lateral view. Scale bar equals 1 mm.

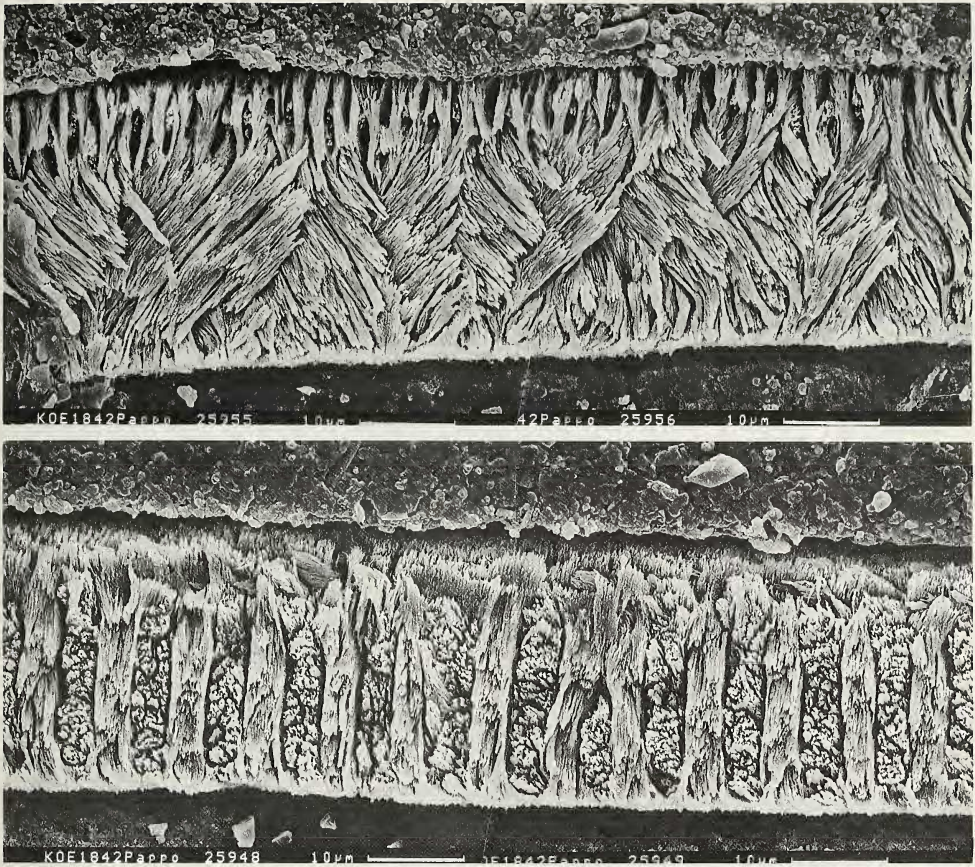


Fig. 5.—Detail of uniserial incisor enamel of *Pappocricetodon antiquus*, IVPP V 11018.611. Above, transverse section; below, longitudinal section.

The cheek teeth are brachydont and have slightly elongate cusps and weak lophs (Fig. 6). M^1 is trapezoidal in occlusal view, the buccal wall slightly longer than the lingual. Its anterior lobe is small with an anterocone that is usually distinct but small. An anterior cingulum extends from the anterocone to in front of the protocone. The protocone is bulbous, and rarely has a weak crest on the posterobuccal side (11/143). As in *P. rencunensis* and *P. schaubi* it extends slightly more buccad than the hypocone. Usually the protoloph is long (128/141) and reaches the anterocone (121/141), but in few specimens it is short and free (13/141). The protoconule on the protoloph ranges from moderate (87/143) to indistinct (56/143). Paracone and metacone are elongate transversely and subequal. The lingual crest from the paracone is weak (119/143) or absent (24/143); if present it intersects the protoloph near the protoconule (90/143) to form a complete protoloph I, or the anterior end of the mure (29/143). There is no trace of a protoloph II. The metaloph is complete and joins the mure near the hypocone. The hypocone is crescentic. Its anterior arm tapers to form the mure, which is usually long and extends far forward, variably meeting the protoloph (39/143), the lingual crest from the paracone (38/143), or the buccal side of the protocone (21/143); it may also end freely (35/143). Occasionally (6/143) it is short and joins the posterior side of the protocone. In V 11018.38, V 11018.40, V 11018.72, and V 11018.127 the mure forks into two branches: one reaches to the protocone and the other to protoloph I to enclose a small basin. The mesoloph is less well-developed than in *P. rencunensis* and *P. schaubi*, is usually short (107/143), or even absent (11/143). It is usually transverse and from medial in position to closer to the metaloph. In V 11018.38 it is oblique and extends from the intersection of the metaloph and the mure. The mesostyle is usually distinct. In some M^1 (56/135) the mesostyle has a lingual crest. The long mesoloph may be formed by a crest from the mesostyle and the short mesoloph. The mesocone is rarely present (7/143). The anterostyle may be distinct (65/139) or indistinct (74/139) and in some M^1 (25/65) it joins the protoloph. The posteroloph reaches the metacone.

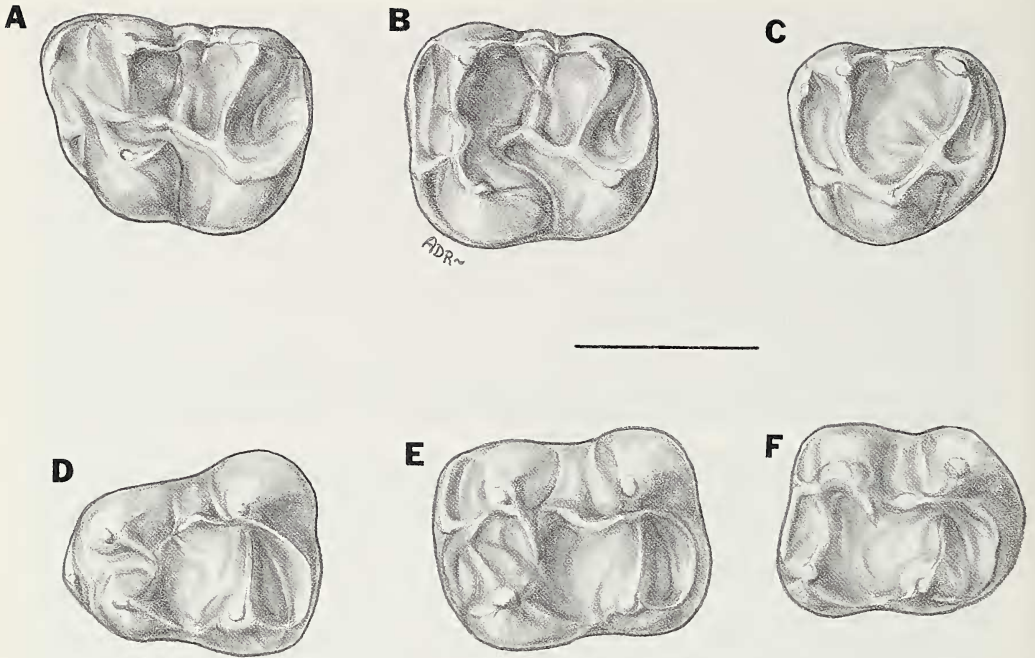


Fig. 6.—Cheek teeth of *Pappocricetodon antiquus*. A. Left M^1 , holotype, IVPP V 11018.1; B. left M^2 , IVPP V 11018.147; C. left M^3 , IVPP V 11018.296; D. right M^1 , IVPP V 11018.419; E. right M^2 , IVPP V 11018.555; F. right M^3 , IVPP V 11018.590.

M^2 is rectangular in occlusal view, slightly longer than wide. The anterior cingulum crosses the anterior wall and joins the paracone buccally. It has a thickened anterostyle anterior to the protocone that becomes a small bridge following wear. As in M^1 the protocone is usually bulbous and rarely (23/143) has a weak crest on its posterobuccal corner. Protoloph I is complete (137/141), and appears to be formed by contributions from the protocone and the paracone. In about half of the specimens of M^2 (60/141), the intersection of the two crests can be seen. In some M^2 the crest from the protocone meets the paracone and leaves a free crest from the paracone anterior (4/141) or posterior (9/141) to it. In V 11018.189, V 11018.240, V 11018.273, and V 11018.277, for example, protoloph I is incomplete because the two crests do not intersect. The mesostyle is usually present (105/140) and has a lingual crest extending toward the mesoloph. The mesoloph may be absent (16/140), short (33/140), or of midlength (69/140). It may be forked (3/102) or double (26/102), with the anterior arm shorter than the posterior. The long mesoloph of some specimens (22/140) appears to be formed by the lingual mesostyle crest joining the short mesoloph. The mure is long, its anterior end usually turning lingually to the buccal side of the protocone (78/143); it may extend to protoloph I (16/143) or end in the valley (25/143). Occasionally it is short, reaching the posterior side of the protocone (3/143). A weak entostyle or crest is sometimes present (51/143), very rarely forming a lingual cingulum that joins the anterior cingulum (7/143). In some M^2 (21/143) the posterobuccal crest of the protocone may meet the mure to separate the lingual valley into open lingual and closed buccal parts.

M^3 , the smallest of the upper molars, varies considerably, especially in talon length and cusp development. The anterior cingulum, paracone, protoloph I, and protocone are well-developed. In some M^3 (6/21), the anterior cingulum wraps around the lingual side of the protocone. The talon is not as reduced as in *P. rencunensis* and *P. schaubi*. The mesostyle is usually distinct but weak (16/21) and the mesoloph varies from weak (9/21) to absent (12/21). In the trigon basin there may be a longitudinal crest (9/21). The metacone varies from cusped to crescentic. The hypocone is less buccal than in *P. rencunensis* and *P. schaubi*. The metaloph is shorter than the protoloph I and usually complete (17/21), enclosing a small basin with the posterior cingulum. The lingual valley is shallower than in *P. rencunensis* and *P. schaubi*.

Of the three lower molars, M^2 is the largest. M^1 has a narrow trigonid as in *P. rencunensis*. Protoconid,

metaconid, hypoconid, and entoconid are similar in size and height, with buccal and lingual cusps aligned transversely. The metaconids are cusped. Most protoconids (89/113) are cusped, some are crescentic (24/113). Metalophid II is usually complete (94/113), formed by the posterior arm of the protoconid (81/113) or joined by a weak crest from the metaconid (13/113). Rarely it is incomplete (17/113) or absent (2/113). The anteroconid is a distinct cuspule that varies from rounded to elongated transversely (105/110). It is more weakly developed than in *P. rencunensis* and *P. schaubi*, usually is low and isolated (89/105) and lacks a distinct cingulum (61/105), has a weak cingulum (one lingual or buccal in 22/105), or has lingual and buccal cingula (18/105). It may be connected with the protoconid (12/105) or the metaconid (4/105). The mesostylid is distinct; it may be isolated (75/110), join the metaconid (31/110), or join both metaconid and entoconid (4/110). The mesolophid is less well-developed and may be very short (49/113), of medium length (31/113), or even absent (29/113). Rarely is it long (4/113). The mesoconid is more weakly developed than in *P. rencunensis* and *P. schaubi*, and either distinct (73/113) or absent (40/113). The ectolophid is usually complete (95/113) and straight (85/95). A few are curved (10/95), in which case the mesoconid is oblique, the anterior arm of the ectolophid is not in line with the posterior arm and is usually more weakly developed. In a few M_1 the ectolophid is incomplete and interrupted in front of the mesoconid (11/113), behind it (4/113), or is completely absent (3/113). In the latter case, the mesoconid is isolated. The hypolophid is usually complete (110/113). It differs from that in *P. rencunensis* and *P. schaubi* in being transverse and joining the hypoconid (93/113), or ending freely (3/113). In some M_1 it extends posteriorly to the posterolophid (6/113) or meets the anterior arm of the hypoconid (11/113). The posterolophid rarely has a buccal part (11/113). Although the hypoconulid is usually absent (96/113), in some it is prominent (17/113) and ends freely (3/113). In V 11018.396 the hypoconid also has a free posterior arm.

The M_2 is nearly rectangular in occlusal outline. As in M_1 the four main cusps are subequal. The lingual cusps are slightly elongate transversely and aligned with the buccal cusps. The protoconid is usually crescentic, as in *P. schaubi* but unlike *P. rencunensis*. The anteroconid is a swelling lateral to the midline on the anterior cingulum. After wear it forms a bridge joining the protolophid near its intersection with the metalophid (137/149). The metalophid connects with the protolophid (120/150), the protoconid (3/150), or the anteroconid (2/150) to form a complete metalophid I (125/150). Occasionally it is incomplete and has a free buccal end (25/150) and leaves the trigonid basin open anteriorly. Metalophid II, formed by the posterior arm of the protoconid, meets the metaconid to close the trigonid basin (89/150), or is free, leaving the trigonid basin incompletely open (61/150). Metalophid II is no greater than medium length and never reaches the lingual margin of M_2 . The mesostylid is distinct (121/149) and variable, being isolated (98/149), connecting with the metaconid (25/149), the entoconid (1/149), or both (6/149). The mesolophid is either shorter than metalophid II (93/151) or absent (57/151). In one specimen, V 11018.461, it is double. The mesoconid is oblique or transverse in orientation (70/150). Although the ectolophid is usually complete (119/150), it varies from straight (69/150) to Z-shaped (50/150). In the latter case, the ectolophid is separated by the oblique mesoconid into an anterior part that is slightly more external and lower than the posterior part. In the few specimens in which the ectolophid is incomplete, the anterior part is very low or absent (24/150) or the posterior part is very low (2/150). In five M_2 (V 11018.449, V 11018.453, V 11018.491, V 11018.498, and especially V 11018.560) anterior and posterior parts of the ectolophid are almost absent and the mesoconid is isolated and elongate transversely. The ectomesolophid is absent (122/150) or weak (28/150). As in M_1 , the hypolophid is usually complete (147/150) and transverse, joining the hypoconid (95/150) or the posterior arm of the hypoconid (4/150). In some M_2 (48/150), the hypolophid meets the anterior arm of the hypoconid. The hypoconulid is usually absent (136/150). In one specimen (V 11018.467), the hypoconulid ends freely.

M_3 is a little smaller than M_1 and M_2 . The trigonid is similar to that of M_2 . The posterior arm of the protoconid is usually free (21/30). It is variable in length, midlength (13/30), short (12/30), or long (2/30). Rarely it is absent (3/30). The mesostylid is either present (14/30) or absent (16/30). The mesolophid is absent (27/30) or very weak and short (3/30). The mesoconid is absent (10/30) or variably present (20/30) and shaped as in M_2 . The ectolophid is variable as in M_2 . Unlike *P. rencunensis* and *P. schaubi*, the ectomesolophid is absent (25/30) or very weak (5/30). The hypolophid is shorter than in M_2 and usually meets the anterior arm of the hypoconid (17/30). However, in some M_3 the hypolophid joins the hypoconid (5/30), the posterolophid (5/30), or is free (3/30).

Comparisons: *Pappocricetodon antiquus* resembles the two other described species of the genus, *P. rencunensis* and *P. schaubi*, and differs from other cricetidids in having relatively less enlarged M^1 and M_3 ; M^1 with a smaller anterior lobe and anterocone, protoloph I present but protoloph II absent, long protoloph usually joining anterocone; M_1 with short and narrow trigonid and small anteroconid; M_3 less reduced.

Pappocricetodon antiquus is smaller than *P. rencunensis* and *P. schaubi* (Table 1). It also differs from these species in having upper molars with a bulbous protocone and a less well-developed mesoloph;

Table 1.—Measurements (in mm) of *Pappocricetodon antiquus*.

		n	O.R.	\bar{x}	s	C.V.
M ¹	Lb	62	1.2–1.55	1.38	0.08	5.8
	LI	62	1.05–1.48	1.24	0.08	6.45
	W	62	0.95–1.25	1.10	0.07	6.36
M ²	L	60	1.15–1.55	1.31	0.07	5.42
	W	60	1.0–1.35	1.13	0.06	5.13
M ³	L	18	0.92–1.15	1.09	0.08	7.61
	W	18	0.87–1.1	1.03	0.06	6.21
M ₁	L	54	1.1–1.4	1.26	0.06	4.76
	W	54	0.8–1.05	0.94	0.05	5.32
M ₂	L	70	1.15–1.45	1.34	0.07	5.22
	W	70	0.9–1.2	1.05	0.07	6.67
M ₃	L	29	1.05–1.4	1.24	0.09	7.26
	W	29	0.87–1.15	1.02	0.06	5.88

M¹ less enlarged (M¹ length/M² length in *P. antiquus*, 1.05; in *P. rencunensis*, 1.12; in *P. schaubi*, 1.18), with a smaller anterior lobe and anterocone, resulting in the relatively less elongated buccal side; M¹⁻² with a long mure and a long, oblique lingual valley; M³ less reduced with a more distinct metacone, an indistinct, less buccad hypocone, and a shallower lingual valley; lower molars lacking ectomesolophid, having a rather transverse hypolophid that joins the hypoconid or posterolophid; M₁ less enlarged and having a less developed anteroconid (M₁ length/M₂ length in *P. antiquus*, 0.94; in *P. rencunensis*, 0.95; in *P. schaubi*, 0.98); M₃ less reduced. Except for the less distinct hypocone of M³, the features mentioned above are primitive.

The incisor enamel of *P. antiquus* demonstrates an early stage in formation of the uniserial type, which is characteristic of myomorphs (W. von Koenigswald, letter, 17 December 1993): "Compared to modern cricetids two primitive characters are found in *Pappocricetodon*. The orientation of the Hunter-Schreger-Bands (HSB) is vertical toward the enamel dentine junction (EDJ), and the interprismatic matrix (IPM) is parallel to the prisms of the HSB. In modern cricetids the HSB are inclined toward the occlusal surface and the IPM is (in lower incisors) oriented at right angles to the prisms in the third direction. The schmelzmuster of *Pappocricetodon* is more derived than in any paramyid or ischyromyid because of the uniserial HSB but primitive compared to modern cricetids."

Relationships: *Pappocricetodon* was originally described as a new genus of cricetid based on isolated teeth (Tong, 1992). No mention was made by Tong of the dental formula of this cricetid. As described above, *Pappocricetodon antiquus* is known to have a tiny P⁴ (or dP⁴). Reexamination of *P. rencunensis* and *P. schaubi* has shown that two M¹ of *P. rencunensis* (IVPP V 8928.6 and V 8928.20) have an anterior wear facet similar to that found in *P. antiquus*, indicating presence of a tooth anterior to M¹. Thus, not only *P. antiquus* but also *P. rencunensis* had P⁴ (or dP⁴) and the dental formula of *Pappocricetodon* appears to have been $\frac{1.0.1-0.3}{1.0.0.3}$. The rudimentary P⁴ (or dP⁴) might have been shed during life.

One of the characters differentiating muroids from dipodoids is absence of P⁴ in the former. Because *Pappocricetodon* has P⁴ (or dP⁴), it could be asked whether or not *Pappocricetodon* is correctly assigned to the Muroidea. A basically similar molar pattern in primitive muroids (Cricetidae) and dipodoids supports the concept of a monophyletic origin of the Myomorpha (Wilson, 1949a, 1949b; Lindsay, 1968, 1977; Martin, 1980; Vianey-Liaud, 1985). The similarity is such that at least one genus, *Simimys*, has been transferred back and forth several times between these two myomorph superfamilies. Clearly, the primitive condition for the myomorphs must include P⁴. P⁴ of *Pappocricetodon* is very reduced. More important than its presence as a primitive feature are derived dental characters shared by *Pappocricetodon* and other cricetids but absent in dipodoids. These include: 1) M¹ has a distinct anterior lobe and anterocone; and 2) the anteroconid of M₁ is transversely elongate and has a cingulum. *Pappocricetodon* has a large, rounded infraorbital foramen, as in dipodoids and some other cricetids such as *Cricetops*, but lacks a neurovascular canal, which is a derived feature of dipodoids. Thus, derived dental features of *Pappocricetodon*, especially in the structure of the first molars, support its reference to the Cricetidae and the most primitive known genus of the family, close to the separation of muroids and dipodoids. The dipodoids are differently derived, retaining the primitive P⁴ and rounded infraorbital foramen, but developing a protective bony septum to form a neurovascular canal.

ORIGIN OF THE CRICETIDAE

Now that *Pappocricetodon* has been recognized as the earliest and most primitive known member of the family Cricetidae, hypotheses on the paleogeographic and phylogenetic roots of this family, long discussed (numerous papers from Schaub, 1925, through Tong, 1992), should be further tested. Characters of *Pappocricetodon* important in this connection are: 1. hystricomorphous-sciurognathous zygomasseteric structure; 2. anterior part of zygomatic plate nearly horizontal; 3. P^4 (or dP^4) present; 4. upper molars with bulbous protocone; 5. mesoloph(id) short; 6. metaloph contacts anterior arm of hypocone; 7. M^1 and M_1 not enlarged; 8. M^1 with small anterior lobe and anterocone; 9. protoloph I weak on M^1 ; 10. protoloph II absent; 11. protoloph short and free buccally on M^1 ; 12. mure free on M^{1-2} ; 13. lingual valley long and oblique on M^{1-2} ; 14. M^3 and M_3 slightly reduced; 15. M^3 with distinct metacone; 16. hypocone distinct, lingually located on M^3 ; 17. posteroloph complete on M^3 ; 18. M_1 with narrow trigonid and small anteroconid; 19. ectolophid absent or incomplete; 20. mesoconid oblique or transverse; 21. transverse hypolophid joins posterior arm of hypoconid; 22. incisor enamel uniserial.

Paleogeographically, the origins of the cricetids and other myomorphs can surely be sought in the Holarctic. In support of this premise is, of course, the occurrence of *Pappocricetodon* in the middle to late Eocene of Asia. To this can be added presence of a myomorph (Dawson et al., 1990) and a ?zapodid (Emry and Korth, 1989) in the early middle Eocene of North America, of *Simimys*, certainly a myomorph and probably a dipodoid, in the later Eocene of North America (Wilson, 1949a; Lindsay, 1977; Emry, 1981), and of some diversity of cricetids in the Chadronian and equivalents of North America and Eurasia. The family is not known from Africa until the Miocene and from South America until the Pliocene.

The Asian rodent record prior to the appearance of *Pappocricetodon* includes the families Alagomyidae in the earliest Eocene of Mongolia and Paramyidae in the middle Eocene of Nei Mongol. (Two species of the Eocene genus *Zelomys* were described as members of the family Sciuravidae by Wang and Li, 1990, but this assignment is still equivocal). Alagomyids and paramyids are generally primitive rodents. Alagomyids lack a hypocone on the upper molars. Paramyids have upper molars with usually well-developed conules, weak lophs from paracone and metacone converging toward the protocone to form a fairly well-marked trigon, and usually only a trace of a hypocone. In both families the lower molars have a pronounced basin. Neither has derived characters suggestive of close relationships with myomorphs. Also present in Asia were several families of the superfamily Ctenodactyloidea, first known from the early Eocene, which have been proposed as myomorph relatives (Lindsay, 1977; Flynn et al., 1985; Vianey-Liaud, 1985; Wang and Meng, 1986). Ctenodactyloids include the protrogomorphous early Eocene *Cocomys* (Cocomyidae) and hystricomorphous middle Eocene *Birbalomys* (Chapattimyidae), *Yuomys* (Yuomyidae), and *Tamquammys* (Tamquammyidae). Among them *Cocomys* and *Tamquammys* are similar to the cricetids in some primitive features such as having upper molars with a free buccal end of the protoloph and some development of a hypocone. Differences between them and cricetids are, however, more prominent: in the ctenodactyloids the cheek teeth increase in size from first to third molars; the upper molars are wider than long; the metaloph extends toward the protocone, forming a trigon similar to that of paramyids; a metaconule is present; the lower molars have a large, distinct hy-

poconulid; and the incisor enamel is pauciserial-multiserial or multiserial. To date no evidence has been found in derived characters to connect *Cocomys* or other tenodactyloids to even the primitive cricetid *Pappocricetodon antiquus*.

European Eocene rodents are paramyids, chapattimyids (Pelaez-Campomanes and Lopez Martinez, 1993), glirids, and theridomorphs. Characters separating paramyids and chapattimyids from cricetids are mentioned above. Glirids are clearly related to the paramyid microparamyines (Hartenberger, 1971). The most primitive theridomorphs, members of the family Pseudosciuridae, occur first in the middle Eocene. These rodents are hystricomorphous and develop uniserial enamel. P³ is absent, the upper molars have a well-developed hypocone, the mure is oblique and separated into anterior and posterior parts. A prominent feature is large P⁴ and P₄, which are never reduced. Even primitive theridomorphs differ from cricetids in having very well-developed conules, transversely-oriented main cusps on upper and lower molars, and only a rudimentary lingual valley. These differences from cricetids indicate no close affinity between these two groups.

North American early and middle Eocene rodents include paramyids, cylindrodontids, sciuravids, and some probable myomorphs. As mentioned above, paramyids show no tendency toward developing lophate teeth with well-developed hypocone and hypolophid that would be expected in relatives of the cricetids. Cylindrodontids do have a well-developed hypolophid, but their upper molars remain on a basic paramyid level of development throughout the Eocene.

The North American rodent family that stands out in dental morphology to have important features shared with the cricetids remains the Sciuravidae (Wilson, 1949*b*). Sciuravids are basically primitive rodents, combining a dental formula of $\frac{1,0,2,3}{1,0,1,3}$, protrogomorphous/sciurognathous zygomaseteric structure, pauciserial incisor enamel, and brachyodont cheek teeth. In molar morphology, however, some sciuravids possess derived characters shared with early myomorphs including the primitive cricetid *Pappocricetodon* and the primitive ?zapodid *Elymys*. In the upper molars conules are reduced; protocone and hypocone are subequal and separated lingually by a pronounced valley; protoloph and metaloph are oblique, extending into the valley anterior to the corresponding para- and metacone. This last character is especially strong in *Sciuravus nitidus*, *S. altidens*, and *S. powayensis*. In *S. bridgeri* the valley between protocone and hypocone is crossed by a low crest from each cusp (Dawson, 1968:350–351). In the lower molars of *Sciuravus* the cusps are set obliquely, with lingual cusps anterior to the corresponding buccal cusps, the ectolophid is complete, the hypolophid is well-developed and the entoconid is separate from the posterolophid. There is a tendency among sciuravids toward reduction of the premolars, seen most markedly in *Sciuravus? rarus* (Wilson, 1938), AMNH 12118 (Dawson, 1962), and *Pauromys*. The Sciuravidae are here considered to be the sister group of the myomorphs (Fig. 7).

Two early middle Eocene North American genera are probably myomorphs. *Armintomys tullbergi*, the oldest known rodent with a hystricomorphous zygomaseteric structure, has incisor enamel that is transitional from pauciserial to uniserial. It seems to be a primitive myomorph but is probably not a member of the Dipodoidea (Dawson et al., 1990) because it lacks the derived neurovascular canal characteristic of that superfamily. It shares with *P. antiquus* some features, such as M¹–M² longer than wide, mesostyle present, low loph, hypocone subequal to protocone, and bipartite metaloph. It is more primitive than *P. antiquus* in some other features including the presence of P³, probably well-developed P⁴, and

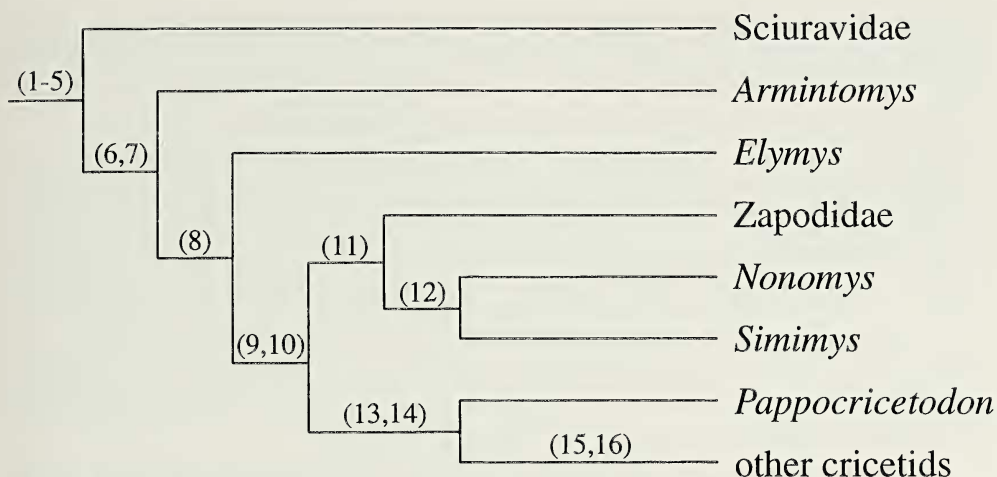


Fig. 7.—Analysis of relationships between the Sciuravidae and several myomorphs, including *Pappocricetodon*, based on characters considered to be shared-derived (synapomorphous) at the branching points: 1, upper molars with hypocone subequal to protocone; 2, upper molars with buccal cusps anterior to corresponding lingual cusps; 3, conules weak or absent; 4, well-developed hypolophid; 5, complete ectolophid; 6, hystricomorphy; 7, pauciserial toward uniserial enamel; 8, P³ absent, P⁴ small; 9, uniserial incisor enamel; 10, zygoma slightly inclined; 11, neurovascular canal separate from infraorbital foramen; 12, P⁴ absent; 13, M¹ with anterocone and anterior lobe; 14, M₁ with anteroconid and anterior cingulum; 15, P⁴ absent; 16, zygomatic plate developed.

lower crowned teeth. Its sciuravid-like molar pattern, hystricomorphy, and incisor enamel indicate that *Armintomys tullbergi* may represent the closest known sister group to a unit including dipodoids and cricetids.

Elymys (Emry and Korth, 1989) from the early Bridgerian of North America resembles *Pappocricetodon* in dental formula and tooth morphology having P⁴ reduced, upper molars longer than wide, oblique compressed protocone and large hypocone, protoconule present in M¹ but lacking in M²⁻³, M¹ with protoloph extending anterobuccally and a protoloph I, M² protoloph I complete, formed by crests from paracone and protocone. *Elymys* is more primitive than *P. antiquus* in having lower-crowned teeth and lacking the mesoloph(id), anterocone and anterior lobe on M¹, and anteroconid on M₁. Because the zygomasseteric structure and incisor enamel of *Elymys* are unknown, its relationships remain uncertain. The suggestion proposed by Emry and Korth (1989:9) is that *Elymys* may be ancestral to both *Simimys* and later zapodids. *Elymys* and *Pappocricetodon* appear to converge toward a common origin.

Simimys, from the Uintan and Duchesnean of North America, combines a hystricomorphous skull with a separate neurovascular canal as in dipodoids but the muroid dental formula of M₃/M₃. It has been regarded as a “more or less primitive survivor into the late Eocene of a stalk which was ancestral to both cricetids and the Dipodoidea” (Wilson, 1949a:23). Recently it has been included in the Dipodoidea (Emry and Korth, 1989). *Nonomys*, from the Chadronian, is another rodent having the derived feature of a separate neurovascular canal. Like *Simimys*, it has the muroid dental formula, but its teeth appear to have a highly derived pattern, cuspsate and with well-developed cingula, very different from the more dipodoid-like pattern in *Simimys*. Although dental features have been used

to support the affinities of *Nonomys* with the muroids (Emry, 1981), the phylogenetic importance of the neurovascular canal is here emphasized and this genus is regarded as a dipodoid.

PALEOGENE CRICETIDS IN ASIA

In the Paleogene of Asia cricetids are represented by eighteen species distributed among four genera: *Pappocricetodon* Tong, 1992 (Middle to Late Eocene of Henan, Shanxi, and Jiangsu provinces, China); *Eucricetodon* Thaler, 1966 (Early to Late Oligocene of Nei Mongol, Gansu, and Yunnan of China, Mongolia and Kazakhstan); *Cricetops* Matthew and Granger, 1923 (Middle Oligocene of Nei Mongol of China, Mongolia and Kazakhstan); and *Selenomys* Matthew and Granger, 1923 (Middle Oligocene of Nei Mongol of China and Mongolia). (Note: *Aksyiromys* and *Ulkenulastomys*, known from one tooth each, were cited as "Myomorpha, family indet." by Shevyreva, 1984. Whatever their affinities, they are apparently not cricetids and accordingly are not considered here.)

Pappocricetodon, the most primitive cricetid, includes three species: *P. rencunensis* Tong, 1992, *P. schaubi* (Zdansky, 1930), and *P. antiquus*, described above, now the earliest and most primitive member of this genus. In most features *P. antiquus* is more primitive than the other two species, but it has a more reduced hypocone on M^3 than *P. rencunensis* and *P. schaubi*, and thus appears to be a sister group to the two latter.

Eucricetodon is represented by ten taxa in Asia: *E. asiaticus* (Matthew and Granger, 1923; Lindsay, 1978) from the Middle Oligocene of Mongolia and Kazakhstan; *E.* near *E. asiaticus* from the Middle Oligocene of Mongolia; *E.* aff. *E. asiaticus* from the Late Oligocene of Kazakhstan; *E. caducus* (Shevyreva, 1967) from the Middle Oligocene of Nei Mongol of China and Kazakhstan; *E.* aff. *E. caducus* from the Late Oligocene of Kazakhstan; *E. meridionalis* Wang and Meng, 1986, and *E. leptaleos* Wang and Meng, 1986, from the Early Oligocene of Yunnan, China; *E. youngi* Li and Qiu, 1980, from the Early Miocene of Qinghai, China; *Eucricetodon* sp. from the Late Oligocene of Taben Buluk, Gansu, China (Bohlin, 1946), and *Eucricetodon* sp. from the Early Oligocene of Mongolia (Janovskaja et al., 1977).

Tong (1992:6-7) considered *Eucricetodon meridionalis* to be more similar to *Pappocricetodon* than to *Eucricetodon* on the basis of the following shared features of tooth morphology: M^1 with a very small anterior lobe, a well-developed protoloph joining anterocone with protocone, and a single anterocone; small M_1 about same length as M_2 and with small anteroconid and trigonid; no free arm of hypoconulid. Tong concluded that *E. meridionalis* was more closely related to *Pappocricetodon* than to other cricetids and might be in the same evolutionary lineage as *P. rencunensis* and *P. schaubi*. However, *E. meridionalis* is here considered to be a species of *Eucricetodon* that has more primitive features than other species of *Eucricetodon*. All the similarities mentioned by Tong are primitive features. In comparison with *Pappocricetodon* and *Eucricetodon*, *E. meridionalis* shares with the latter such derived features as M^1 having an enlarged anterior lobe, a large anterocone, lacking protoloph I but having a complete protoloph II, a large anteroconid, and M_1 longer than M_3 . *E. meridionalis* is here retained in *Eucricetodon*.

Tong (1992:7) also doubted the position of *E. leptaleos* in *Eucricetodon* because he thought it had the following special characters: 1) short protoloph (=anterior arm of protocone in Tong, 1992) extending towards paracone or joining crest

from paracone (=protoloph in Tong, 1992); 2) anterocone(id) small and with a smooth posterior surface; 3) absence of a bridge from anterostyle (=caudaler anteroconussporn of Dienemann, 1987, and Tong, 1992); 4) M^3 having simple structure; 5) M_1 equal to M_2 in length; 6) weak lophs on lower molars; and 7) M_3 with a reduced talonid. Of these, 1, 2, 3, 5, and 6 are primitive features of cricetids and similar to those of *Pappocricetodon*, and 4 is variable in cricetids and probably not phylogenetically significant. Only 7 is a derived feature but it is shared by *Eucricetodon*. In fact, in *E. leptaleos* the anterior lobe of M^1 is enlarged and forms a distinct lobe, the anterocone is large, and protoloph II has begun to form, as in *Eucricetodon*. Thus, *E. leptaleos* appears to be a primitive species of *Eucricetodon*.

Pappocricetodon rencunensis and *P. schaubi* share some derived features: a long protoloph joining the anterocone on M^1 , a well-developed mesoloph, and a buccal hypocone on M^3 . These features differ from those of *Eucricetodon*, including *E. meridionalis* and *E. leptaleos*, and other later cricetids. However, among the cricetids *Eucricetodon* is closest to *Pappocricetodon*. Possibly primitive cricetids in Asia may have divided into two lineages, with *Pappocricetodon* representing a primitive group, and another lineage represented by *Eucricetodon* and other Asian cricetids, in which M^1 and M_1 are enlarged and have a large anterocone(id) and M_1 has a well-developed anterior cingulum. There remain many gaps in the history of cricetids in Asia, however, with such problems as the origin of *Cricetops* and the peculiar *Selenomys* still to be resolved.

PALEOGENE CRICETIDS IN THE HOLARCTIC

Now that the geologically oldest and morphologically most primitive cricetid rodents are known to occur in the Eocene of Asia, implications of the entirely Holarctic Paleogene stratigraphic and biogeographic record of the family should be reconsidered. *Pappocricetodon* is important in providing evidence on primitive characters of cricetids that allows a clearer understanding of character polarity among Paleogene forms. No attempt is made here to revise the family at the subfamily or any other level. Currently the infrafamilial arrangement of cricetids can conservatively be characterized as in a state of flux (contrast, for example, the familial and subfamilial associations of Martin, 1980, Ünay-Bayraktar, 1989, and Freudenthal et al., 1992).

Cricetids appeared in Europe after the Grande Coupure. Since that event cricetids (sensu lato) diversified and dispersed rapidly in Europe. Thirteen genera are recognized (Freudenthal et al., 1992) in the European Paleogene record. The earliest cricetid is *Eucricetodon atavus* from Hoogbutsel (the *Eucricetodon atavus* tooth from the pre-Grande Coupure locality Mohren 6 should be dismissed due to faunal mixing within the fissure, following the discussion in Dienemann, 1987). It resembles the Asian *E. meridionalis* in size and some aspects of tooth morphology, but is more derived in having first molars with a larger anterior lobe and anterocone(id) and more reduced third molars. The record supports the hypothesis that *Eucricetodon* migrated from eastern Asia into Europe after the Grande Coupure.

In North America, as in Europe, a major cricetid radiation occurred in the Oligocene (*Eumys* sp. described by Storer, 1988, from the Duchesnean of Saskatchewan has been referred to the Sciuravidae by Dawson, in press), from which eight cricetid genera have been reported (Martin, 1980). They have some common features, such as more or less swollen main cusps, short posteroloph and well-developed metacone on M^3 , which differ from those of Asian Paleogene cricetids,

including *Pappocricetodon* and *Eucricetodon*. The North American cricetids *Eoemys*, *Scottimus*, *Leidymys*, *Geringia*, and *Pacculus* are not referable to the Eurasian Eucricetodontinae (Tong, 1992, contra Martin, 1980). The Oligocene genera *Geringia* and *Pacculus* have a small anterocone-anteroloph that differentiates them from contemporary North American cricetids. This state has been regarded as a reduction from the *Eumys* condition. The morphology of the primitive Asian *Pappocricetodon* opens the possibility that these genera represent another immigration from Asia rather than a reduction from North American endemic rodents.

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